REVIEWS / SYNTHÈSES

Predicting and managing light in the understory of boreal forests[1]

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Abstract: This paper reviews current information relating to the dynamics of light in northern and boreal forests and discusses factors affecting overstory light transmission, seasonality of light, sunflecks, canopy gaps, and understory development, particularly with regard to tree regeneration. Techniques for measurement of light in forests such as radiometers, photosensitive paper or chemicals, hemispherical canopy photographs, the plant canopy analyzer, or visual estimators of canopy density are each discussed in terms of their accuracy, costs, ease of use, and conditions required during measurement. Predictive models of light transmission based on canopy architecture are also described in terms of their assumptions, accuracy, and input data costs. Lastly the paper discusses the relationship among overstory and understory densities, ground-level light, and "windows of opportunity" for regeneration of trees in the understory following management interventions.

Résumé : Cet article passe en revue les connaissances courantes sur la dynamique de la lumière dans les forêts nordiques et boréales. Les auteurs y discutent des facteurs qui affectent la transmission de la lumière dans le couvert, les variations saisonnières de la lumière, les trouées de lumière, les trouées du couvert et le développement du sous-étage, particulièrement en relation avec la régénération des arbres. Les diverses techniques de mesure de la lumière, telles que l'utilisation de radiomètres, de produits chimiques ou de papiers photosensibles, de photographies panoramiques du couvert, d'analyseurs de la composition du couvert ou d'estimateurs visuels de la densité du couvert, sont analysées sur la base de leur précision, de leur coût, de leur facilité d'utilisation et des conditions requises pour effectuer les mesures. Les modèles de prédiction de la transmission de la lumière qui reposent sur l'architecture du couvert sont aussi décrits en fonction des hypothèses sur lesquelles ils reposent, de leur précision et du coût d'acquisition des données. Finalement, les auteurs discutent des relations entre la densité de l'étage dominant et celle du sous-étage, de la lumière au niveau du sol et des circonstances opportunes pour la régénération des arbres en sous-étage suite à des interventions d'aménagement.

[Traduit par la Rédaction]

Introduction

Photosynthetically active radiation (PAR), i.e., between 380 and 710 nm (Larcher 1980), is fundamental for photosynthesis and growth of understory plants (Canham et al. 1990; Sims and Pearcy 1993; Chen and Klinka 1997). While other spectral bands are important for the thermal environment in the forest understory (Bunnell and Vales 1990; Black et al. 1991), this review focuses on visible light (380–770 nm) and PAR, which, owing to the similarity of their spectral range, are often used synonymously. Stand density and light interception (Goetz and Prince 1996) are the critical factors controlling the stages of forest stand development and the establishment of saplings in the understory of forests (Oliver and Larson 1990) and are the variables most often considered in predicting establishment and growth of regeneration following partial cutting (Nyland 1996; Smith et al. 1997).

A synthesis of the large body of literature on light dynamics in forest stands is timely, given the renewed interest in partial-cut silvicultural systems, management of mixed-species stands and the desire to establish trees in partial shade. We review issues related to light in boreal and northern forests, especially with regard to conditions for the establishment and growth of tree seedlings. These high-latitude sites (i.e., >45°N) are characterized by short summers with relatively low maximum solar elevations and long winters with very low solar elevations. This paper describes

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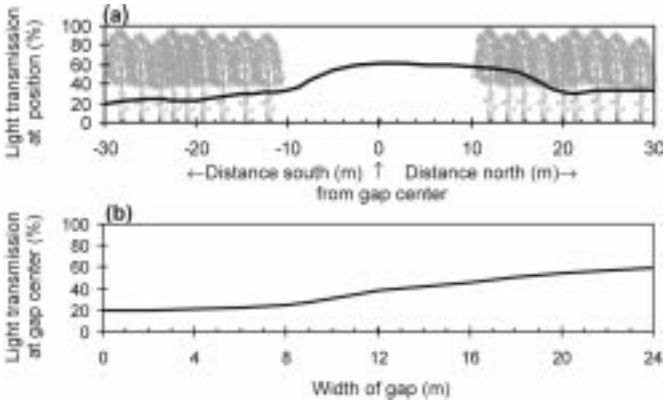
Fig. 1. (*a*) Effect of gap position on seasonally integrated light transmission. This gap is 24 m wide in a homogeneous birch stand 10 m in height (Comeau et al. 1998). (*b*) Effect of gap size on seasonally integrated light transmission at the gap center (Comeau et al. 1998).



canopy-level and microsite-level light regimes and the techniques for measuring and estimating light at each of these scales. We review the dynamics of overstory light transmission diurnally, annually, and during stand development, the spatial heterogeneity and spectral quality of light, the interception of light by understory shrub and herb layers, the different techniques for measuring light and simulation models for prediction of light, and lastly the application of this knowledge to the management of forests and directions for future work.

Dynamics of light in forests

Overstory light transmission

Light in forests is constantly changing in both intensity and direction (Anderson 1964; Norman and Jarvis 1975; Gay et al. 1971; Baldocchi and Collineau 1994) because of the earth's daily and annual celestial movements relative to the position of the sun. The apparent path of the sun relative to a position on the earth's surface can be described geometrically in relation to season and time of day (Duffie and Beckman 1974). These differences and the constant change in cloud cover result in a wide variation in incoming light above forest stands. When tree, shrub, and herb canopies of various size, shape, and opaqueness are present on a site, the amount of light penetrating the canopy is further changed.

Diffuse light, which emanates from other parts of the sky as a result of scattering of sunlight by the atmosphere, varies in significance with latitude, angle from the horizon, cloud cover, and pollution. The forward scatter of light striking aerosols in the atmosphere can increase the amount of diffuse light on days when the sky is not completely clear (Monteith and Unsworth 1990). This same effect causes a 5–10 % increase in total light on days with broken cumulus clouds, during the times when the sun is not covered by cloud (Monteith and Unsworth 1990). While there are some differences in the amount of diffuse light emanating from various parts of the sky (Grant 1985; Wang and Jarvis 1990), for simplicity, it is commonly assumed that each sector of the sky dome is uniformly luminous (Canham et al. 1994). On days with complete cloud cover, the hemispheric origin of the light means that there is much less spatial and temporal variation in light within the forest (Messier and Puttonen 1995; Parent and Messier 1996). In addition to light coming directly from the sky, some PAR passes through the leaves themselves or is reflected downward by the foliage. On clear days, scattering of sunlight by this process is called beam enrichment (Hutchison and Matt 1976) and can represent 15% of midday radiation coming through the overstory and 40% of radiation below the shrub layer (Hutchison and Matt 1976) in deciduous stands or 14–41% of the overstory transmission for hardwood- or conifer-dominated stands (Canham et al. 1994). Others (Gay et al. 1971; Vales and Bunnell 1988*a*) have inferred beam enrichment from an increase in the proportion of diffuse light under the canopy compared with the proportion above, but this may be confounded by the differential absorption of diffuse light relative to direct light, which depends on the inclination of foliage and sun angle even in the absence of scattering (Oker-Blom 1986).

Seasonality of light

Seasonal differences in canopy light transmission are driven by differences in solar elevation, day length, and phenology of the vegetation (Hutchison and Matt 1977; Uemura 1994). Because some broad-leaved trees carry foliage only in the summer, their effect on reducing the percentage of above-canopy light is highest in summer (Hutchison and Matt 1977; Constabel and Lieffers 1996). There are also seasonal differences in boreal spruces and pines of 5–10% because of timing of needle flush and cast (Chen 1996). Measurement of light in spring and fall is important because some evergreen species in the understory may be able to photosynthesize during the periods when the hardwoods are leafless; indeed, Emmingham and Waring (1977) estimated that 50% of the annual photosynthesis of conifers in the Pacific Northwest occurs between October and May. In the cold winters of the boreal forest, evergreen species are not photosynthetically active (Jurik et al. 1988; Man and Lieffers 1998). The periods of hardwood leaf-off in April and early May and in late September and October, however, are also important for photosynthesis of understory white spruce (Man and Lieffers 1997) and evergreen boreal forests herbs (Landhaüsser et al. 1997). Also, while light in the winter months may not be directly important for photosynthesis, bright light in conjunction with freezing temperature may damage photosystem II (Lundmark and Hällgren 1987).

Canopy gaps, sunflecks, and spatial heterogeneity

Large gaps in the canopy permit long periods of uninterrupted transmission of direct-beam light to the understory (e.g., Runkle 1981; Canham 1988; Canham et al. 1990). Canopy gaps create a range of light conditions within and around the gap opening depending on the sun angle, tree height, and sky condition (Canham et al. 1990; Messier 1996). As the size of an opening increases, the amount of light reaching the center of the gap also increases as a function of both the diameter of the gap (Fig. 1*b*) and the height of the surrounding stand, i.e., the sky view factor. At night, the sky view factor is related to radiation loss to the sky and the occurrence of summer frosts (Groot and Carlson 1996).

Table 1. Sunfleck threshold, duration of measurement period, and percentage of daily light on sunny days contributed by sunflecks for a range of northern forests.

Authors	Stand type and location	Sunfleck threshold ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Duration of measurement	Sunfleck % contribution to total PAR
Chen and Klinka 1997	Douglas-fir, Pacific Northwest	50	<18 days	32
Messier and Puttonen 1995	Mature Scots pine, Finland	90	4–7 days	90
Messier and Puttonen 1995	Open 7-year-old Scots pine, Finland	350	4–7 days	65
Lei and Lechowicz 1990	Eastern deciduous	100	Samples over 16 days	53
Messier et al. 1998	Boreal forests of eastern Canada	100	One full sunny day	
	Aspen			59
	White birch			75
	Three deciduous–coniferous stands			60–70
	Fir – white spruce			79
	Black spruce			69
	Jack pine			86
Messier et al. 1998	Mixed boreal forests of Quebec	250	One full sunny day	
	Aspen			28
	White birch			53
	Mixed deciduous–coniferous			51–57
	Fir – white spruce			56
	Black spruce			32
	Jack pine			49

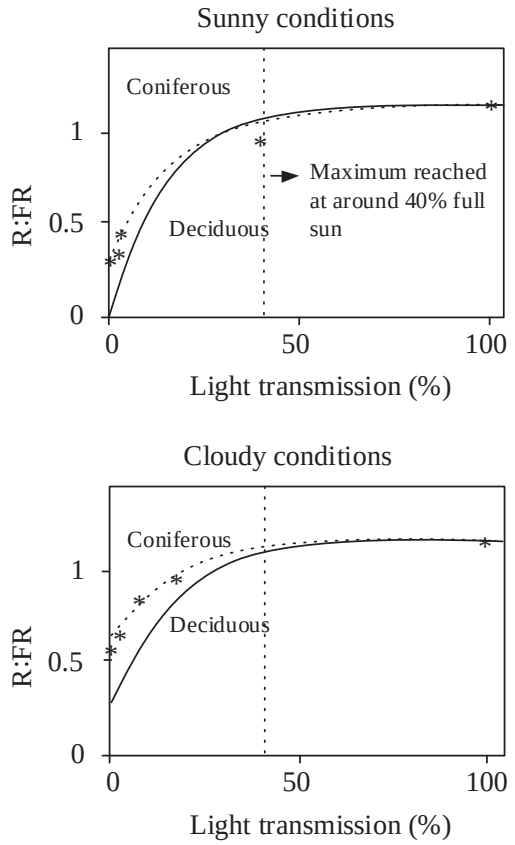
Even in relatively uniform stands with a relatively dense overstory, there is significant spatial variation in light transmitted to the understory. Hutchison and Matt (1977), Kikuzawa (1992), and Messier et al. (1998) noted a positively skewed distribution of light in the understory, presumably because of similar variation in overstory structure. Thus, even in stands with few apparent canopy gaps, there are some understory positions with higher light regimes where seedlings could be established. At present, there is a shortage of information on the range of light regimes in understory and its effects on forest dynamics.

In high-latitude sites, because of the low solar elevation, the location of high radiation at ground level is offset relative to the gap center (Canham 1988; Canham et al. 1990; Dai 1996). Thus, in the Northern Hemisphere, the south edge of a forest opening will receive diffuse light from the northern portion of the sky, while the northern edge of the gap will receive both diffuse and direct-beam light (Canham et al. 1990; Bazzaz and Wayne 1994) (Fig. 1*a*). At high latitudes and if trees are tall, the effectiveness of the small to moderate-sized gaps for creating regeneration habitats may be compromised, as the area of increased light does not coincide with the area of reduced competition for water and nutrients. Given that most boreal forest species have relatively narrow crowns (Kuuluvainen and Pukkala 1989), once gaps are created, further growth of crowns is less likely to close the canopy gaps. In eastern deciduous forests, by comparison, crown expansion into gaps is an important factor (Runkle 1981; Hibbs 1982; Runkle and Yetter 1987; Valverde and Silvertown 1997).

Sunflecks can be defined as a small patch on the forest floor that on a sunny day receives a substantial increase in the amount of direct-beam light relative to the general forest floor (Chazdon 1988). As some canopies transmit much more light than others, the application of the above qualitative definition results in a range of thresholds for sunflecks (Table 1). Unfortunately, different choices of threshold result in different estimates of the importance of sunflecks, making it difficult to distinguish between the effects of different thresholds and real differences in sunfleck importance. To illustrate this, Messier et al. (1998) found a sunfleck contribution of 60–86% of daily PAR using a 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ threshold and 28–75% with a 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ threshold over a full sunny day in midsummer in closed boreal forest stands (Table 1). Logically, it might be better to select sunfleck thresholds that are related to the photosynthetic light–response curve of important understory plants. We also suggest that it is most appropriate to estimate the importance of sunflecks over at least one full range of daylight hours on completely clear days. Other studies have estimated that sunflecks contribute anywhere from 32 to 90% of daily PAR (Table 1), but these estimates are subject to the concerns raised above.

Sunflecks resulting from small, concrete canopy openings are of relatively short duration and relatively low intensity because of penumbral effects. The penumbral effect is related to the fact that direct-beam radiation is not from a point source, i.e., the solar disc and aureolus have area. At a distance 50–70 times the diameter of the opening in the canopy, the center of the sunfleck drops below full light intensity and the opening is entirely penumbra (Horn 1971; Smith et al. 1989; Oliver and Larson 1990). Smith et al. (1989) suggested the use of this ratio (gap size/distance to the incident opening) to differentiate among sunflecks (<0.01), sunpatches (>0.01 but <0.05), gaps (>0.05 but <1.0), and clearings (>1.0). Thus, many small openings in the canopy of tall trees will result in a relatively uniform and diffuse light at ground level. This has been described as high shade (Chapman 1944). Tree seedlings in high shade are known to loose epinastic control of terminal buds resulting in a shrublike

Fig. 2. Idealized relationships between R:FR and photosynthetic photon flux density under coniferous- versus deciduous-dominated stands under completely sunny or cloudy conditions. The lines drawn for coniferous stands under sunny and cloudy conditions are based on data from Messier and Puttonen (1995) under pure Scots pine stands in Finland and on data points (asterisks) from Messier et al. (1989) under pure stands of western hemlock and western redcedar. These relationships were also checked with data from Ross et al. (1986), Mailly and Kimmins (1997), and Ritchie (1997). The line for deciduous stands under sunny conditions is based on continuous data points covering the range from 1 to 100% full sunlight collected under pure stands of broadleaf maple in coastal British Columbia by F. Gendron (unpublished data) and data from Morgan and Smith (1981), Messier and Bellefleur (1988), Endler (1993), St-Jacques and Bellefleur (1993), and Lei et al. (1998). The line for deciduous stands under cloudy conditions is based on data from Morgan and Smith (1981), Messier and Bellefleur (1988), Endler (1993), and Lei et al. (1998).



form of trees in deeper shade (Oliver and Larson 1990). The mechanism for this is not clear, but it may relate to the uniform intensity of the light as much as to the low total daily irradiance (Oliver and Larson 1990) or the modifications in the quality of light beneath large versus small canopy holes (Endler 1993).

The uniformity of light plays a role in seedling development. An environment of uniform but moderate shade produced larger seedlings than an environment with lower light for most of the time but with periods of high light due to sunflecks, even though the daily total irradiance was the same (Wayne and Bazzaz 1993; Sims and Pearcy 1993). In essence, the periods of very strong light cannot be fully used, as the light levels exceed the linear quantum yield portion of the light–response curve (Sims and Pearcy 1993). Secondly, in some forests, sunflecks may have a median duration as short as 2 s (Chazdon and Pearcy 1991). To take advantage of these brief periods of higher light, the photosynthetic system of plants must be induced by recent exposure to strong light. This may take as long as 20–60 min (Chazdon and Pearcy 1991), although in Douglas-fir, 90% induction of understory-adapted trees may occur in as little as 63 s (Chen and Klinka 1997). For shade leaves, especially of late successional species, induction can be maintained by a series of light pulses (Küppers et al. 1996). In many woody species, stomata remain open during short periods of low light, while in many herbaceous species, stomata track light levels, closing during periods of low light and opening rapidly in response to high light (Knapp and Smith 1990). Given the variation in understory environments within and among stands, there is opportunity for development of specialists to exploit these light environments. However, because the boreal forest is a relatively young (<12 000 years) community (Ritchie 1978), species with specialized physiological strategies may not have had time to develop. For example, *Calamagrostis canadensis* is able to survive in aspen understories but will close its stomata during brief dark periods and requires 2 min of strong light induction to begin reopening them (Greenway and Lieffers 1997); thus, it is not particularly well suited to take advantage of brief sunflecks.

Light quality

Forest canopies absorb or reflect much of the PAR while transmitting most of the far-red part of the spectrum (aprroximately 730 nm) (Larcher 1980). Different canopy structures result in differences in the quality of transmitted light (Endler 1993); in sunny conditions, light under a full canopy is yellow to green, small sunflecks are dominant in the red part of the spectrum, while large gaps produce white light (Endler 1993; Turnbull and Yates 1993). One of the most common ways of summarizing spectral quality is the red to far-red ratio (R:FR), i.e., the ratio between transmitted light in the red band (655–665 nm) to far-red light (725–735 nm) (Larcher 1980). In general, R:FR declines with increasing canopy density (Messier et al. 1989). On sunny days, this decline is steeper than on cloudy days (Endler 1993; Messier and Puttonen 1995). This has been noted for hardwood stands (Messier and Bellefleur 1988), Scots pine (Messier and Puttonen 1995), radiata pine (Morgan et al. 1985), and mixed conifers (Federer and Tanner 1966). On sunny days, R:FR may vary from 0.1 under dense eastern hardwoods (Messier and Bellefleur 1988) to 1.0 in large gaps (Turnbull and Yates 1993; Lei et al. 1998) and from 0.4 under dense conifer canopies to 1.0 in large gaps (Messier et al. 1989; Messier and Puttonen 1995; Ritchie 1997; Mailly and Kimmins 1997). Generally, hardwood canopies have a lower R:FR than conifer canopies (Ross et al. 1986; Messier and Bellefleur 1988; Messier et al. 1989; Messier and Puttonen 1995), suggesting better absorption of red light by hardwoods. Figure 2 summarizes these observations and proposes idealized relationships for both pure deciduous and coniferous species on both completely sunny and cloudy days.

While plants have photoreceptors specific for ultraviolet and blue radiation (Aphalo and Ballaré 1995), the most common mechanism by which plants respond to changes in light quality is through the phytochrome system (Smith 1982), which is influenced by R:FR (Larcher 1980). Seed germination, stomatal opening, and leaf and stem morphology of many plant species are affected by this ratio (Smith 1982; Endler 1993), but trees that are commonly found in understory conditions (Smith 1982; Bazzaz and Wayne 1994; Kitajima 1994; Lee et al. 1996) are less likely to respond to changes in R:FR. Light quantity alone, however, seems to have a much more pronounced effect on tree growth and physiological acclimation to shade than light quality (Kitajima 1994; Lee et al. 1996).

Light in relation to stand development

As a stand reaches crown closure, i.e., the stem exclusion phase (Oliver and Larson 1990), light transmission to the understory declines sharply. After this stage, there is an increase in overstory light transmission for aspen (Lieffers and Stadt 1994; Constabel and Lieffers 1996), Scots pine (Messier and Puttonen 1995), and eastern hardwoods (Brown and Parker 1994) as leaf area declines with age. Aspen stands in Minnesota, however, did not show a decline in leaf area with age up to approximately 100 years (Goetz and Prince 1996). In spruce–aspen mixedwoods, the higher the percentage composition of spruce in the overstory, the less light is transmitted to the understory (Lieffers and Stadt 1994; Constabel and Lieffers 1996). Constabel (1995) noted that light transmission through the crowns of single spruce trees was one half to one-tenth that of aspen trees of similar stem size. Canham et al. (1994) and Messier et al. (1998) also observed that shade-intolerant species (either deciduous or coniferous) transmit more light than shade-tolerant species, presumably because of a thinner crown.

The ability of trees to support leaf area and thus intercept light decreases with environmental stress (Waring and Schlesinger 1985). Aspen stands in Quebec therefore transmit less light than the same stand types in Alberta, possibly because of the greater annual precipitation in eastern forests (Messier et al. 1998). In general, light transmission is higher for boreal forests with their cold conditions than for the warmer and wetter temperate deciduous forests (Messier and Bellefleur 1988; Canham et al. 1990; Brown and Parker 1994) or conifer forests of the Pacific Northwest (Messier et al. 1989). Messier (1996) found in closed boreal forests that light transmission above the shrub layer varies from 2 to 40% whereas in temperate and coastal forests, it is usually less than 5%.

Light transmission through shrub and herb layers

The effect of shrubs and herbs on the light regime at ground level is also important, as this is where seedlings must start their life. Germination of seedlings on elevated microsites such as rotten logs or mounds (DeLong et al. 1997) elevates the seedlings above some of the shading by the herbaceous layer and may improve their growth and survival. Tree seedlings gradually grow up through the shrub and herb layers, thereby overtopping this shading leaf area and improving their prospects. Minimum light levels required for survival, however, may also increase as a sapling becomes larger (Givnish 1988; Messier 1996).

Shrub and herb layers in boreal forests may be virtually nonexistent when there is a dense overstory canopy of conifers (Rowe 1955; DeGranpré et al. 1993). In contrast, these layers may be very vigourous under older aspen stands in which the leaf area of the understory might even be greater than that of the overstory (Constabel and Lieffers 1996). As a general rule, understory leaf area is inversely proportional to overstory leaf area (Cannell and Grace 1993). If the overstory captures much of the incoming light, little remains to support the understory (Rowe 1955; Constabel and Lieffers 1996). In Alberta mixedwood forests, light transmission to ground level was 6% of above-canopy PAR in three mixedwood types of different age and overstory composition (Constabel and Lieffers 1996). Similarly in Quebec, transmission to ground level below the understory was 2% in an aspen stand, 7% under birch and pine, and 4% under a late successional stand of balsam fir and red spruce (Messier et al. 1998).

Light transmission and competition indices have been recorded for several shrub and herbs that are competitors in clear-cut conditions (Vose and Swank 1990; DeLong 1991; Comeau et al. 1993; Ter-Mikaelian et al. 1997) or in open fields (Hirose and Werger 1995; Tournebise and Sinoquet 1995). Since leaf inclination and leaf area likely change in the understory, new information must be gathered for understory conditions. Annuals show a peak in leaf area in late spring, while most perennials maintain their leaf area over the summer (Uemura 1994). Given that some shrubs and herbs are deciduous and others evergreen (Uemura 1994), and given the differences in the persistence of and position of leaf litter (Hogg and Lieffers 1991), the amount of shading caused by green leaves and litter will vary seasonally.

Measurement of light in forests

The following six subsections discuss methods used to estimate light penetration to the forest understory. The first three methods measure light directly through use of quantum sensors or chemical techniques. Light transmission refers to the ratio of PAR measured at some point within the stand compared with PAR incident on the canopy, usually measured in an adjacent clearing or on a tower with a near-complete hemisphere of skyview. These measure transmission of direct and diffuse light, as well as beam enrichment. The other three techniques measure light indirectly through an estimation of canopy openness or gap fraction. These are simplified measures of light transmission: openness is a measure of diffuse skylight transmission (Chazdon and Field 1987) and gap fraction measures diffuse skylight or direct-beam transmission (Norman and Campbell 1989). Both terms ignore the effects of beam enrichment.

Light meter measurements

Continuous seasonal measurements

Continuous recording of light transmission to a particular microsite, both diurnally and seasonally, using quantum sensors and dataloggers is clearly the best method of characterizing the light environment of that microsite over a

particular time period. It also provides information on the temporal variation in light. These continuous recordings are often used as the reference light transmittance for comparison with other methods of light estimation (Rich et al. 1993; Easter and Spies 1994; Gendron et al. 1998). Most quantum sensors record light between 400 and 700 nm (Pearcy 1989). For most purposes, this is considered to approximate the range of PAR (Larcher 1980). While other sensors measure energy flux density (irradiance), Pearcy (1989) suggested that PAR sensors better describe the light necessary for plant growth. Commercially available quantum sensors can be used, but the number of microsites that can be measured is usually limited by the cost of the sensors. An alternative is to make low-cost sensors using gallium arsenide phosphide (GaAsP) photodiodes (Pearcy 1989; Pontailler 1990; Rich et al. 1993; Easter and Spies 1994; Gendron et al. 1998). These lightweight sensors can even be mounted on individual leaves (Gutschick et al. 1985). The number of randomly positioned sensors required for canopy-level estimation depends on the precision required. Reifsnyder et al. (1971) found coefficients of variation (CV) of 121% for pine and 225% for hardwood values for each sensor averaged over a 5-min period. If averaged over the entire day, however, the CV dropped to 43 and 13.5%, respectively, indicating that fewer sensors are needed to characterize light over days or seasons.

Single-time measurements of light

Measurements can be taken with two quantum sensors, one recording light above the canopy and a second below the canopy. The sensor above the stand is connected to a datalogger, while the sensor in the understory is connected to a handheld radiometer/datalogger. This is a simple and inexpensive method for determining percent PAR.

Measurements on sunny days: Measurements taken near midday in full sun have been widely used for characterizing light (Carter and Klinka 1992; Comeau et al. 1993; Lieffers and Stadt 1994; Smith and Riitters 1994; Wünsche et al. 1995), but the technique is not well suited for estimating light at a particular microsite because of the temporal variation in light due to sunflecks or canopy gaps. The average of two readings, one before and one after solar noon, is a better indicator of the growing season light transmission to a particular microsite (measured by sensors) than one instantaneous measurement taken at noon (R^2 = 0.84 for two measurements compared with R^2 = 0.67 for only one, Gendron et al. 1998). At stand level, estimates of light transmission can be determined by averaging instantaneous measurements from a large number of sampling points distributed within the stand (Lieffers and Stadt 1994). Using a handheld radiometer, Pierce and Running (1988) noted that 30 samples, each the average of 20 measurements with an 80-sensor radiometer (Decagon Devices, Pullman, Wash.) taken in a circular sweep, would have 8–15% error in the estimation of stand leaf area using Beer's Law.

Measurements on overcast days: Instantaneous measurements of transmittance on overcast days using single sensors show stronger correlation with growing season transmittance than midday or entire-day measurements on sunny days (Messier and Puttonen 1995; Parent and Messier 1996; Gendron et al. 1998). Reifsnyder et al. (1971) also noted that on overcast days, fewer sensors are needed to characterize light with the same level of precision as on sunny days. In theory, at high latitudes with their lower solar angles, the probability of penetration of the canopy by direct-beam light may be lower than the average penetration of diffuse light. In practice, however, the daily percentage of above-canopy light that is transmitted by a canopy is similar on clear and overcast days (Messier and Puttonen 1995; Parent and Messier 1996). The percentage of light transmitted to the understory is stable over the day under overcast skies (Messier and Puttonen 1995). Consequently, the average light transmission at a given point during the growing season (measured using seasonal readings of a quantum sensor) can be estimated from a single instantaneous light measurement taken during overcast sky conditions. In contrast with the hemispherical canopy photographs and LAI-2000 methods (see below), light measurements on overcast days using quantum sensors record the total light in the understory, i.e., diffuse light that comes unimpeded from the sky as well as light reflected and transmitted by the vegetation. Also, as long as the entire sky is covered uniformly by clouds, light measurements can be taken any time during the day. However, owing to the asymmetry of direct-beam penetration into a gap or around opaque crowns, a diffuse light measurement may under- or overestimate seasonal light transmission (Messier and Parent 1997; Stadt et al. 1997; Gendron et al. 1998) in these situations.

Photosensitive paper (ozalid paper)

Light-sensitive diazonium salts on ozalid paper are bleached on exposure to light. When developed with ammonia vapor, the bleached portions of the paper stay white, while the rest turns color (Francis 1970). The number of layers of paper bleached is proportional to the light energy received (Friend 1961). Normally, the ozalid paper is left in the understory at particular microsites for a complete day to estimate the integrated daily total radiation value (Kanemasu et al. 1971; Emmingham and Waring 1973; Cole and Newton 1986). Ozalid paper installed in the understory is compared with similar paper installed in an adjacent open area. The technique does not provide a direct measure of PAR, but results are expressed as a percentage of light transmission. The advantage of this technique over others is that large numbers of microsites can be sampled by stacks of ozalid paper in petri dishes, thus providing information on both the microsite and stand level. Although relationships between photochemical measurements and measured light are good (R^2 = 0.99, Friend 1961), the sensitivity of ozalid paper peaks in the blue and ultraviolet range of the spectrum, which is not directly related to the spectral bands used in photosynthesis (Pearcy 1989). Ozalid paper can be used in clear and overcast conditions. Use of neutral density filters increases the period of integration and the accuracy of readings and decreases the variation among samples (Francis 1970).

Price et al. (1995) used Sunprint photosensitive paper for measuring light interception for selected branches in grape canopies. Similar to the ozalid paper, the Sunprint paper becomes blue under exposure to light. The number of blue pixels, analyzed using an image analysis system, is related to

light intensity. It is therefore possible to obtain a spatial distribution of light intensity for a short period of time (approximately 5 min). Light estimates from the Sunprint paper and a PAR quantum sensor are highly correlated (R^2 = 0.93), but the spectral response of the Sunprint paper is unknown. The method allows for measurement of spatial variation of light on small surfaces, and papers can be easily shaped to the measured leaves or shoots. Chemical processing, image scanning, and analysis are time-consuming.

Photochemical methods

Photochemical methods (Marquis and Yelenosky 1962; Wolfenden et al. 1982; Kurachi and Hagihara 1994) typically use a jar of chemical solution that changes color or solubility on exposure to light and have been used to estimate PAR in forest canopies under both clear and overcast conditions. These changes are quantified with a spectrophotometer or analytical balance and then related to the quantity of light received during a given period. Correlations between photochemical light estimates and measured light are strong (R^2 = 0.99, Marquis and Yelenosky 1962), but solutions are also influenced by ultraviolet radiation. As with ozalid papers, sensitivity of the solution does not exactly correspond to the region of the spectrum used in photosynthesis (Pearcy 1989). Photochemical methods are an inexpensive alternative to estimating light simultaneously at several microsites. However, Wolfenden et al. (1982) and Kurachi and Hagihara (1994) have reported some potential problems when using potassium ferrioxalate and anthracene–ethyl solutions. Time spent on the preparation of the solutions and processing with the spectrophotometer adds to the costs of these techniques.

Hemispherical canopy photographs

Photographs of canopies taken with a 180° field-of-view lens (Evans and Coombe 1959) are scanned and analyzed with image analysis software to calculate below-canopy percent light transmission, sunfleck distribution, R:FR, percentage of canopy openness, and leaf area index (Chazdon and Field 1987; Chen et al. 1991; Rich et al. 1993; Easter and Spies 1994; Wünsche et al. 1995; Gendron et al. 1998). The photographs provide a permanent record of overstory canopy geometry relative to an understory position. Analysis of hemispherical canopy photographs allows users to track the movement of the sun over the day and the entire growing season, thereby providing detailed estimation of PAR penetration. Algorithms for analyzing canopy photographs, such as the gap light index (Canham 1988), give only the percentage of light transmission to the understory, which has been shown to be strongly correlated with measured growing season light transmission (R^2 = 0.95, Gendron et al. 1998). Most software used for analysis of hemispherical photographs underestimates background diffuse light found in the understory (Chazdon and Field 1987). Since these programs calculate only light that comes unimpeded from the sky, penumbral light and light scattering are not considered in the calculation of understory light. Some automated analysis programs can be calibrated by long-term sensor measurements to give more accurate prediction of transmitted light (Rich et al. 1993; Whitmore 1993; Easter and Spies 1994). Also, it is difficult to apply this technique in stands with tall shrubs. Despite use of computers and image analysis software, data processing is time-consuming. Careful light exposure is important for successful photographs (Chen et al. 1991). Taking photographs under overcast sky conditions or early in the morning and late in the afternoon increases the contrast between the leaves and the sky and facilitates the determining of light threshholds (Chen et al. 1991).

Diffuse light transmission using the LAI-2000 plant canopy analyzer

The LAI-2000 plant canopy analyzer is designed to estimate leaf area index but can also provide an estimate of diffuse light transmission (Gower and Norman 1991; LI-COR 1992) to a particular microsite. It has a 150° field-of-view lens positioned above five concentric light-detecting silicon rings that receive radiation from five different zenith angles (LI-COR 1992). A filter rejects radiation above 490 nm, so the contribution of radiation scattered and transmitted by foliage is minimized. The LAI-2000 can be used in clear sky conditions with view restrictors that block direct-beam light. Under completely overcast sky conditions, light estimates calculated with the LAI-2000 and the hemispherical canopy photographs are strongly correlated (R^2 = 0.97, Thormann 1997). LAI-2000 measurements on days with variable sky conditions are also correlated (R^2 > 0.91) with growing season light transmission (Gendron et al. 1998). Even though the LAI-2000 records only light below 490 nm, these studies demonstrate that diffuse transmission is directly related to PAR in a forest understory. Hanan and Bégué (1995) have also used the LAI-2000 to develop a model for estimating direct light transmission from diffuse noninterceptance. The model effectively simulated the daily variations in light transmission. In the field, the LAI-2000 is easily manipulated. As with hemispherical canopy photographs, beam enrichment is not detected by the LAI-2000, which may result in the underestimation of PAR, especially under shade-tolerant species. One difficulty with the LAI-2000 is obtaining a suitable outside canopy measurement. Users need stable light conditions during the period of measurement or a second LAI-2000 to log conditions outside the canopy while taking readings under the canopy (Welles 1990).

Visual estimators of canopy density

The principle of the spherical densiometer (Lemmon 1956) and the horizontoscope (Schütz and Brang 1995; Thormann 1997) is similar to the hemispherical canopy photograph method. For both devices the image of the canopy above a forest position is projected onto a spherical mirror. The spherical mirror of the densiometer is divided into 24 squares, while the horizontoscope has a hyperbolic dome mounted on the top of a circular surface. Each is handheld and the user visually assesses the amount of the sky not covered with the silhouette of vegetation. The spherical densiometer can be used to estimate the gap fraction, while the horizontoscope can also be used to estimate the duration of direct light and percentage of diffuse light transmission received at a particular microsite. Horizontoscope estimates are correlated (R^2 > 0.86, Schütz and Brang 1995; Thormann

1997) with those of hemispherical canopy photographs. However, the horizontoscope is less accurate under a canopy with many small gaps (Thormann 1997). The horizontoscope is easy to use in the field and light measurements can be recorded under both clear and overcast sky conditions. The moosehorn (Robinson 1947) is another handheld instrument where the user visually estimates canopy cover in a narrow field of view directly above the user (Bunnell and Vales 1990). All of these instruments have different angles of view of the sky and this results in different estimates of crown completeness (Bunnell and Vales 1990). Since there is no correction for the length of path of view through the canopy at the various angles, the moosehorn (Robinson 1947) with its narrow angle of view has a lower estimate of crown completeness than the spherical densiometer with a wider angle (Bunnell and Vales 1990).

These techniques have been used to estimate the light regime of specific points in the understory, but since the path of the sun at high latitudes is low in the sky, they are not particularly well suited for spatially explicit light measurements. P.G. Comeau et al. (unpublished data), however, reported a good relationship between spherical densiometer measurements and growing season percent PAR (R^2 = 0.92). With all of these techniques, there is variation in estimates among observers and a training program would be necessary to standardize readings (Vales and Bunnell 1988*b*). A tripod to steady and level the instrument is also recommended.

Models for prediction of light in stands.

Approaches to modeling light beneath forest canopies attempt to link measurements of canopy density and structure to a light transmission probability. The simplest and most widely used approach in agricultural and forestry applications is the Beer–Lambert Law. Its original form is

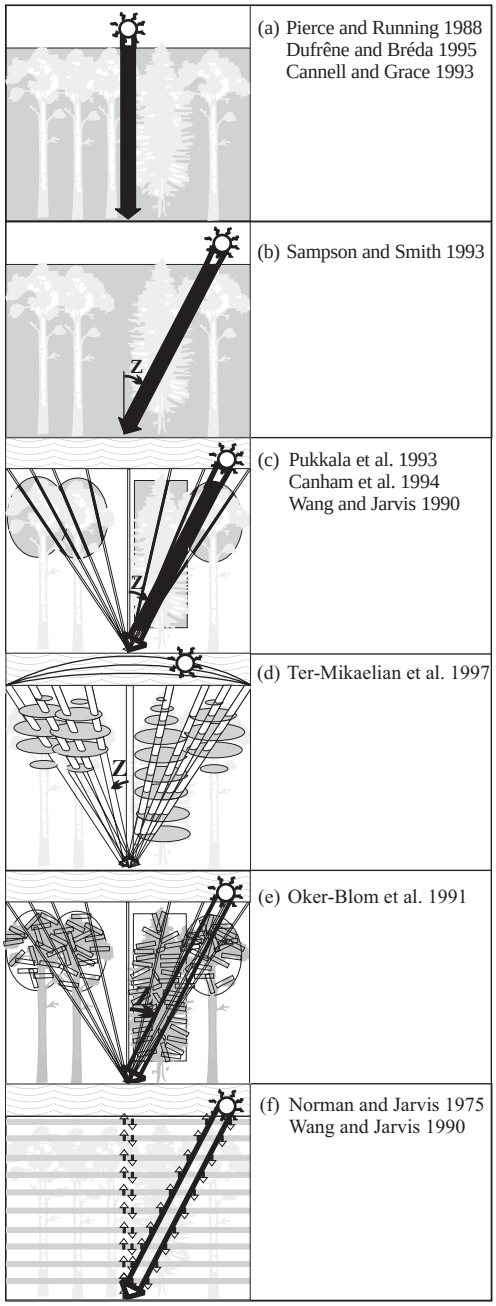
$$(1) \qquad I/I_o = e^{-a \cdot b \cdot c}$$

where I is the light measure at the detector, I_o is the light incident on the absorbing region (I/I_o is the fractional transmission), a is the absorptivity of the objects in the region (dimensionless), b is the path length of the beam through the absorbing region (e.g., in metres), and c is a measure of the "concentration" of the objects (for trees, this could be leaf or wood area density (LAD, WAD, square metres per cubic metre)). The product $a \cdot b \cdot c$ is the absorbance for the region (Swinehart 1962). In ecological applications, some of these absorption parameters are often combined. Key assumptions of the Beer–Lambert Law are that the objects in the absorbing region are randomly distributed in vertical and horizontal space, that these objects reflect and transmit no light, and that the light rays are parallel (Figs. 3*a* and 3*b*). Given the same assumptions, Oker-Blom (1986) demonstrated that the Beer–Lambert Law can be derived from a Poisson process.

The Beer–Lambert Law is applied at various scales depending on the information available. The simplest models treat the entire canopy as the light-absorbing region (Fig. 3*a*) with an extinction coefficient, k, derived from a calibration of light versus leaf area index (LAI, square metres per square metre), i.e.:

$$(2) \qquad I/I_o = e^{-k \cdot LAI}$$

Fig. 3. Pictorial representation of the light transmission models. The actual canopy structure is shown in light gray. The medium-gray area in each frame is the light-absorbing region, which can be (*a* and *b*) canopy, (*c*–*e*) crown, (*e*) shoot, (*e*) leaf, or (*f*) layer. The sources of light are shown above each canopy: the sun (radiating globe), skylight (stippled bar), or "seasonal sky" (stippled bar with the solar track; see text). Paths taken by light from these sources through the canopy are shown by arrows: the wide arrow represents the path taken by direct sunlight and the narrow arrows are diffuse skylight. Where the seasonal sky is the light source, medium arrows are used. Arrows are black where they pass through the models' light-absorbing regions. Z is the zenith angle.



Although it is not apparent, eq. 2 embeds the light path length (b). The extinction coefficient (k) is the absorptivity (a) corrected for its projection on a horizontal plane (i.e.,

$k = a/\cos\theta_z$). LAI should be considered the average leaf area per unit gound area along a narrow path through the canopy from the light source. In a homogeneous canopy, LAI is the concentration or LAD multiplied by the canopy height (i.e., LAI = LAD·h = c·h). Canopy height is a function of the light path length (b) and the cosine of its source zenith angle (θ_z), i.e., $h = b\cdot\cos\theta_z$. Equation 2 is thus consistent with eq. 1. This application of the Beer–Lambert Law was introduced by Monsi and Saeki (1953) and has been widely used. In forestry, its most frequent application is to estimate LAI, rather than to predict light (Pierce and Running 1988; Dufrêne and Bréda 1995), but the inverse can also be effective. Using an independent estimate of LAI, Pierce and Running (1988), for example, found that eq. 2 accurately predicted light transmission in seven conifer stands at two solar angles ($R^2 \geq 0.94$).

Because the equation is relatively simple, a k is required for each stand type. Jarvis and Leverenz (1983) reported a range of values of k from 0.28 to 0.65, determined empirically by inversion of eq. 2 for pure stands of various species at a given solar angle. However, k is known to be affected by the angle of incident light and the leaf angle distribution of the foliage (Campbell 1986; Lang 1987; Black et al. 1991; eq. 5 below), making it difficult to generalize k for other solar angles and species mixtures. LAI must also be determined, either directly, which is time-consuming, or by estimation from relationships between leaf area and sapwood area, which must be established first (Waring and Schlesinger 1985). Most forests are mixtures of species, and therefore, k and LAI should be determined for each species and combined additively in the model (Cannell and Grace 1993):

$$I/I_o = e^{-\sum_{species} k_{species}\cdot LAI_{species}} \quad (3)$$

Further, eqs. 2 and 3 are strictly valid only if the effects of boles, branches, and beam enrichment are ignored, the leaves are randomly positioned in space, and either the leaves are horizontal (i.e., not inclined) or the light originates from one direction (Oker-Blom 1986). Bole and branch wood plays a significant role in light attenuation (Cermák 1989; Chen 1996) but can be accounted for by basing k on plant area index (PAI = LAI + wood area index (WAI)) or adding WAI as another term in the model (cf. eq. 3). WAI can be measured directly (Sampson and Smith 1993) or PAI estimated by light-interception techniques (Dufrêne and Bréda 1995), although for light predictions the latter result is a somewhat circular process. Accounting for nonrandom leaf distribution and leaf inclination requires more effort (see below). The parallel light assumption can be met instead by limiting predictions to clear days when the sun acts as an approximate point source of most of the incident light or by treating the sun and sky as many small sources of light and integrating transmission along numerous paths.

Sampson and Smith (1993) suggested a model that reflects the change in the extinction coefficient k with the solar zenith angle θ_z (Fig. 3*b*):

$$I/I_o = e^{-G/\cos\theta_z\cdot LAI} \quad (4)$$

where

$$G = a = k\cdot\cos\theta_z \quad (5)$$

This formulation extends direct sunlight transmission predictions to all solar angles for predictions at any time of day or season. However, these authors found that G was not independent of LAI in 19 lodgepole pine stands, and thus, eq. 4 predicted light transmission poorly.

A further refinement is to define absorptivity a as a separately measurable foliage projection parameter, conventionally symbolized as G (Nilson 1971). The G and k are interconvertible using eq. 5, and recent studies use either (Campbell and Norman 1989). If the foliage area is inclined as if it were distributed across the surface of a geometric object, such as a sphere or ellipsoid, and the shadow of this object is projected onto a surface perpendicular to the direction of the light source, G is the ratio of the shadow area to the upper surface area of the distribution (Campbell 1986; Oker-Blom 1986). A random azimuth orientation is usually assumed, so that only the inclination from horizontal needs to be considered. Values of G for known distributions are given in Nilson (1971), Campbell (1986), and Oker-Blom (1986) and usually vary with the zenith angle of the light source. When G is ignored, a spherical distribution is implicitly applied, which has a constant G value of 0.5 for all source directions. The highly flexible beta distribution (Goel and Strebel 1984) has also been used to model forest foliage inclination (Wang and Jarvis 1990) but requires numerical techniques to approximate G. Of course, leaf angle is nearly impossible to measure directly on trees, but Norman and Campbell (1989) have developed an iterative inversion process that can parameterize k and LAI (or G and LAD, with appropriate modifications), given a number of measurements of direct sunlight transmission taken at different solar angles.

To extend light predictions to cloudy days or over long periods, the Beer–Lambert Law can be applied to the probability of transmitting a single beam of diffuse light through the canopy from each region of the sky (Figs. 3*c* and 3*e*):

$$i = i_o(\theta_z, \psi)\cdot\cos\theta_z\cdot e^{-G(\theta_z)\cdot b\cdot LAD} \quad (6)$$

where i is the light reaching a horizontal plane at the measurement point, i_o is the light originating from the sky at a given zenith (θ_z) and azimuth (ψ), the cosine of the zenith corrects i_o to light striking a horizontal surface (Lambert's Law), G again is a function of the leaf inclination distribution and the zenith (cf. Oker-Blom 1986), and b and LAD are as defined above. Equation 6 is integrated numerically over the upper hemisphere to calculate diffuse irradiance. Complex functions of the distribution of diffuse sky brightness (i_o) with zenith and azimuth are available (Oker-Blom 1986), but the degree of cloudiness makes the actual distribution uncertain, so it is often assumed that all areas of sky are equally bright (Canham et al. 1994; Ter-Mikaelian et al. 1997). Several studies (e.g., Canham et al. 1994; Ter-Mikaelian et al. 1997) have developed a "seasonal sky" that has sectors whose brightness is the product of the time the solar track passes through the sector, the direct-beam light irradiance at that sector's zenith, and the likelihood of that sector not being obscured by cloud (Fig. 3*d*). Diffuse light could be incorporated into the i_o values for these sectors, so that integration of eq. 6 over these sectors would give the total seasonal light.

The effects of nonrandom distribution of foliage horizontally and vertically within the canopy in simulation studies were found to be the next most important factor after LAI in predicting light transmission (Sampson and Smith 1993; Larsen and Kershaw 1996). An attempt to include between-crown gaps in a Beer–Lambert Law model was not fruitful (Sampson and Smith 1993). Positive and negative binomial distributions or Markov models (Nilson 1971; Sinclair and Knoerr 1982; Oker-Blom 1986) have been suggested as alternatives to the Beer–Lambert Law for nonrandom foliage distributions, but estimating these models' parameters is not straightforward. Pukkala et al. (1993) and Canham et al. (1994) took another approach and used spatially mapped tree crowns, modeled as cylinders or ellipsoids, as multiple light-absorbing regions (Fig. 3*c*). This accounts for gaps and the horizontal aggregation of foliage into crowns. In these models, light transmission depends on the sum of the path lengths within the crowns through which light beams pass on their way from the sky to the measurement point. Pukkala et al.'s (1993) pure Scots pine model used allometrically determined projected LAD (pLAD = projected leaf area per tree divided by crown volume), equivalent to $G \cdot \mathrm{LAD}$, to convert within-crown length (b) into absorption:

$$(7) \qquad i = i_o(\theta_z, \psi) \cdot \cos \theta_z \cdot e^{-\sum_{\text{species}} \sum_{\text{tree}} \mathrm{pLAD}_{\text{species, tree}} \cdot b_{\text{species, tree}}}$$

(Pukkala et al. (1993) multiplied transmission values rather than adding absorbances; these are equivalent.) The absolute path length variant of Canham et al.'s (1994) mixedwood model also combines foliage projection and LAD into species-specific extinction coefficients equivalent to pLAD, except that these were determined by maximum likelihood regression of the sum of the path lengths through crowns of each species on canopy openness as determined by hemispherical photography. The predictions of Pukkala et al.'s (1993) model were correlated with measured light transmission ($r \geq 0.69$) and showed a similar spatial distribution; seedling growth correlated with predicted light as well. For Canham et al.'s (1994) model, predictive accuracy is harder to evaluate. Openness calculated by the model appears to be correlated with the estimate determined from hemispherical photographs, but no independent validation was performed.

Korzukhin and Ter-Mikaelian (1995) also developed a spatially explicit model where individual trees or shrubs are represented by vertical or horizontal planar screens of appropriate shape that are semitransparent to light. The model estimates the amount of light passing through the screens and between the trees to specific ground positions. It is similar in approach to the "hits" variant of Canham et al.'s (1994) model. For species with long crowns and multiple layers, Ter-Mikaelin et al. (1997) refined the model to use multiple horizontal screens, each representing a single uniform layer of leaves with the correct horizontal size and approximate vertical position (Fig. 3*d*). The issue of within-crown foliage distribution can then be addressed as well, particularly for species with tiered, whorled branch structure. With good estimation of leaf area and extinction coefficients for the screens, estimation error was less than 8% of the measured light.

Several other attempts have been made to model within-crown foliage distribution. Norman and Welles (1983) applied the Beer–Lambert Law to nested subcrown regions of different LAD. Individual tree crowns were modeled as nested ellipses, and transmission was calculated as the sum of the subcrown absorbances (projected LAD × path length through each subcrown region):

$$(8) \qquad i = i_o(\theta_z, \psi) \cdot \cos \theta_z \cdot e^{-\sum_{\text{tree}} \sum_{\text{subcrown}} \mathrm{pLAD}_{\text{tree, subcrown}} \cdot b_{\text{tree, subcrown}}}$$

Norman and Jarvis (1975) took cylindrical single-cohort shoots as the light-absorbing region of their Sitka spruce light transmission model. These were grouped into flat, circular whorls positioned along a stem. The proportion of the horizontal area occupied by these whorls when projected toward the light source, the probability of hitting a shoot within a whorl at this angle, the transmission through the shoot cylinder, as well as the contribution of reflection and through-leaf transmission were used to calculate light flux through successive canopy layers (see below). Wang and Jarvis (1990) distributed leaves vertically through the live crown and horizontally from the stem according to density functions fit to harvested trees. Transmission through these trees was calculated as with Norman and Welles (1983). Oker-Blom et al. (1991) developed a hierarchical model of light transmission, in which light can be absorbed by individual leaves, shoots, or crowns (Fig. 3*e*), to determine the relative importance of leaf size, area, and inclination, shoot area and distribution, and stem distribution in the stand to model predictions. LAI was poorly estimated, confounding the analysis, but this paper laid the groundwork for modeling light transmission at any of these levels. The crown-absorption variant of this model produced estimates of light transmission within 8% transmittance of the measured value for four pure lodgepole pine and one Engelmann spruce stand (Oker-Blom et al. 1991).

The contribution of beam enrichment, the reflection and through-leaf transmission of direct sunlight and diffuse light, is the most difficult aspect to model. Canham et al. (1994) calculated direct-beam enrichment as the difference between diffuse light predicted by their model and measured light at times when the sun was shining but not striking the measurement sensor. From this estimate, they suggested that beam enrichment could account for 14–41% of the understory irradiance. Norman and Jarvis (1975) modeled beam enrichment by measuring leaf reflection and through-leaf transmission values and converting these and the leaf distribution information (see above) to vertical upward and downward transmission/reflection coefficients for thin horizontal layers of canopy. To model the entire light environment, an iterative approach was taken. First, upward and downward reflection was evaluated layer by layer from the ground, starting with the soil reflectivity, to the top of the canopy. This yielded a starting ratio of diffuse light tending upward to diffuse light tending downward at each layer. Transmission, reflection, and absorption of diffuse skylight were then evaluated layer by layer from above the canopy to the ground. The process was iterated several more times, but with both direct sunlight and diffuse light fluxes considered, until the upward- and downward-tending light estimates at each layer were stable (Fig. 3*f*). By accounting for leaf transmission and reflection, the direct and diffuse light scattered by each layer could contribute to the layer's estimate

Fig. 4. Understory canopy of (*a*) an intact dense conifer stand, (*b*) immediately after thinning, and (*c*) 5 years later. The dense overstory virtually eliminates the understory. The period after thinning allow increased light to ground level, but this period is short-lived, as the understory eventually colonizes this space.

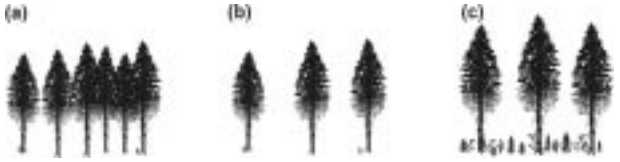
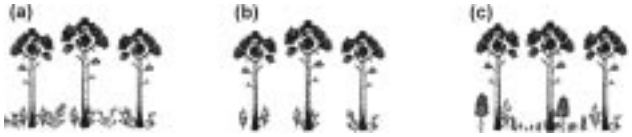


Fig. 5. Understory canopy of (*a*) a mature aspen stand, (*b*) immediately after strip understory site preparation, and (*c*) 5 years later. The porous overstory of the aspen allows a heavy understory to develop. The strip site preparation provides a temporary increase in light to ground level, but the understory eventually redevelops.



of total diffuse flux. The predictive accuracy of this model appears to be good. The stand-average transmission at four heights was predicted closely by the model (fig. 11 of Norman and Javis 1975). Using a modeling approach that combined the Norman and Jarvis (1975) radiative transfer approach with a light ray tracing model similar to Pukkala et al. (1993) and Canham et al. (1994), Wang and Jarvis (1990) found that the difference between predicted and measured transmission for Sitka spruce and radiata pine stands was less than 10%. However, in addition to the required information on the LAD, spatial distribution, and inclination angle distribution, information on transmission and reflectivity of leaves and stems must also be obtained for each species involved.

Application of these models to the estimation of stand development has been hindered by lack of specific calibration data for the individual stands in question. The methodologies listed above for measurement of light within forests are useful for describing individual stands but have not been used for prediction of light in a large number of stands, such as in a forest management unit. High costs for estimation of such factors as foliage inclination, clumping, and stem mapping make some of the above models impractical for application to a large number of stands. Furthermore, the effect of the understory vegetation is not usually taken into consideration, and the spatial (point-by-point) accuracy of many of the models has not been evaluated. As a result, consideration of light transmission and prediction of understory development is usually not incorporated into stand-level planning. A goal for further modeling would be to use the data collected in a normal timber cruise or permanent sample plot, e.g., a stem map with species, diameter, height, height to live crown, crown width, and understory species cover, as the model input.

Management of light in forests

While managers have no control of above-canopy light, they can control the light levels in the understory by controlling the amount, position, and type of vegetation that absorbs the incoming light. The benefits from controlling light include (*i*) promoting establishment and early development of tree seedlings, thereby establishing the next generation of trees, (*ii*) managing the growth of lower strata of trees in uneven-aged and mixed-species management systems, and (*iii*) controlling the growth of understory shrub/herb layers either to suppress their growth as competitors or to promote their growth for wildlife habitat or biodiversity reasons. With an understanding of the density and position of shading leaf area and the way that stands develop naturally, managers can identify or create windows of opportunity for developing appropriate light regimes for these goals suggested by the following examples.

Manipulation of overstory density

In a relatively stable forest system, the biomass of the understory is inversely correlated with the density of the overstory (Zavitkovski 1976; Cannell and Grace 1993; Brown and Parker 1994; Lieffers and Stadt 1994; Ricard and Messier 1996). A long-term strategy for controlling shrub and herb competition during the regeneration phase is to develop dense overstory canopies at the end of the rotation. Persistent competitors such as *Rubus idaeus* (Ricard and Messier 1996) or *Calamagrostis canadensis* (Lieffers and Stadt 1994) can be eliminated from the understory if light is below 10% of above-canopy light. In the subsequent regeneration phase, there may be a delay in the redevelopment of these plants, as they must recruit from seed rather than from a bud bank (Tappeiner et al. 1991). Knowledge of the speed of recruitment and growth of the shrub/herb layer is critical to estimating the period of increased light at ground level following overstory thinning. This has rarely been studied (Hannerz and Hånell 1993).

Reducing overstory density in shelterwood and selection systems or commercial thinning (e.g., Johansson 1987; Oliver and Dolph 1992) temporarily destabilizes the balance between overstory and understory canopies, allowing increased light transmission to the understory and ground surface (Fig. 4). Managers might match the light transmission to the understory with the light requirements for growth of target species. For white spruce seedlings, the light required for maximum photosynthesis of an individual twig is between 40 and 60% of full sunlight (Man and Lieffers 1997), while volume growth is linearly related to light transmission (Klinka et al. 1992; Comeau et al. 1993; Chen et al. 1996). In the regeneration phase, managers may choose to retain a relatively dense overstory and sacrifice some of the growth rates of saplings for several reasons, e.g., (*i*) in dry sites, daytime radiation loading may overheat regeneration if too much overstory is removed (Holbo et al. 1985), (*ii*) in colder areas, nighttime radiation losses and night frosts are reduced in partial-cut areas compared with clearcuts (Groot and Carlson 1996), and (*iii*) when there are aggressive shade-intolerant shrubs, grasses, or herbs, a residual overstory can inhibit their growth more than the height growth of shade-tolerant tree seedlings (e.g., *Rubus idaeus* (Ricard and Messier 1996), *Epilobium angustifolium* and *Calamagrostis canadensis* (Lieffers and Stadt 1994), and *Gaultheria*

shallon (Messier et al. 1989)). Thus, for tree regeneration, the amount of residual canopy could be balanced to deliver sufficient light to allow establishment of the desired trees but avoid competitors and temperature extremes.

The rate at which tree canopies close after partial removal of the overstory will depend on the proportion of the original stand remaining and on the rate of horizontal expansion of crowns (Smith et al. 1997). Over time, this will gradually result in reduction of light to understory layers (Fig. 4), closing the window of opportunity.

Removal of the overstory in patches and strips results in large openings for light transmission (Berry 1964). The orientation of these openings influences the regeneration environment in the understory. At high latitudes, narrow strips oriented east–west will result in patches of strong light under the crowns of adjacent residual trees, and light conditions will be similar to those of small gaps (Canham 1988). Some shelterwood systems orient the cut face east–west to encourage illumination and regeneration under adjacent residual trees (Matthews 1989). Strips oriented north–south will have brief periods of high illumination at noon.

Site preparation of the understory

Removal of the shrub/herb layer by chemical or mechanical means also temporarily destabilizes the understory vegetation, making the overstory the only significant barrier to light (Fig. 5*b*). Blading out the roots and rhizomes of understory plants reduced shading for 5 years (Lees 1970). Provided tree recruitment is early, this period may be sufficient to establish tree seedlings.

Concluding remarks

We have attempted to outline part of the massive body of literature on light in forests, including the different approaches for measuring, modeling, and manipulating light availability and quality in forest stands. Implications for regenerating tree species have been discussed. We now identify a number of areas for further study, listed in the same order of topics as in the review. (*i*) The seasonality of understory light availability in relation to the photosynthetic activity of understory plants needs more work. How much do these plants, particularly regenerating evergreens, improve their carbon gain at the times when the overstory is leafless? (*ii*) Does the importance of gaps in forest dynamics decline with latitude, owing to the spatial offset of the position receiving additional light relative to the region with increased soil moisture and nutrients? (*iii*) Thresholds for sunflecks should be related to the light demands of the understory species. Since sunflecks may not be as significant in well-lit understories, a strategy for sunfleck measurement needs to be developed that recognizes the significance of background light levels. (*iv*) More ecological work should be done to determine the effects of spectral characteristics other than R:FR on understory plant performance. (*v*) The distribution of leaf area and leaf area inclination in the understory canopy and its effects on the light profile for growing trees need further study. (*vi*) Further modeling of beam enrichment in forests is needed to improve the spatial accuracy of indirect light measurements. (*vii*) Simulation models of light transmission should be modified so that standard forest inventory data can be used as input rather than the extensive and specific data required by present models. This would allow light availability to be used as a predictive management tool. (*viii*) Response of forest regeneration following silvicultural treatments such as thinning, partial cutting, or site preparation should be linked to estimates of light at ground level.

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